Genitalia, fluctuating asymmetry, and patterns of sexual selection in *Physocyclus globosus* (Araneae: Pholcidae)*

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Genitalia, fluctuating asymmetry, and patterns of sexual selection in *Physocyclus globosus* (Araneae: Pholcidae). - Some recent papers on sexual selection distinguish between 'secondary sexual traits' and 'other morphological traits'. An analysis of genitalic and non-genitalic characters in a spider revealed that genitalia cannot be assigned to any of these two categories, but rather show a mixed and inconsistent pattern. It is argued that this reflects the multifunctionality of genitalia, which, in the case of complex genitalia like in many spiders and insects, may consist of coupling (including sperm transfer) and displaying structures, each of which are subject to different selective regimes.

Key-words: genitalia - sexual selection - secondary sexual traits - fluctuating asymmetry.

THE NEGLECT OF GENITALIA

When DARWIN (1871) discussed the concept of sexual selection, he mainly concentrated on external courtship and fighting structures of vertebrates (about 80% in the group specific section). Although present day knowledge of invertebrate sexual biology is much larger, most recent insights with respect to sexual selection still emerge from studies on secondary sexual traits of birds, fishes and amphibians (conspicuous plumage, sex-specific coloration, frog-calls, etc). It is not surprising therefore that most theoretical concepts of sexual selection are based on vertebrate secondary sexual traits (FISHER 1930; LANDE 1981; ANDERSSON 1986; POMIANKOWSKI *et al.* 1991; POMIANKOWSKI & IWASA 1993). A new aspect has been introduced into the discussion by EBERHARD (1985), who applied Darwin's ideas to animal genitalia. Thus he was able to explain some extravagances of genital evolution (rapid and divergent evolution, species-specificity, morphological complexity) which were well known to taxonomists for a long time but were previously not convincingly explained.

However, in most current discussions of sexual selection, genitalia are not referred to. In this note I will argue that this neglect may lead to unjustified generalizations as to the way sexual selection operates.

Current discussions of sexual selection often distinguish between 'secondary sexual traits' and 'other' ('ordinary', 'non-sexual') morphological traits (MØLLER & HÖGLUND 1991; MØLLER 1993; MØLLER & POMIANKOWSKI 1993; WATSON & THORN-HILL 1994; SWADDLE & CUTHILL 1994; SIMMONS *et al.* 1995). A number of general differences between the two categories have been put forward. Table 1 lists some of these, following MØLLER (1993). Evidence is not sufficient to assign any genitalic structure unambiguously to one of the two categories in all seven points, but at least two points are beyond dispute: genitalia are usually highly species-specific (point 2) and, from the perspective of survival ability, of low 'functional importance' (point 7). As to point 1 there are both very simple and highly complex genitalia. As regards points 3-6 (direction of selection, developmental stability, patterns of fluctuating asymmetry), investigations into these subjects are badly needed.

THE MIXED PATTERN OF GENITALIA

This note presents data from a morphometric analysis of genitalic and non-genitalic characters in 32 individuals of each sex of the spider *Physocyclus globosus* (Taczanowski, 1873) (Pholcidae), which provide preliminary characterizations with respect to points 3-6 in Table 1. Based on detailed studies of courtship and copulation (Huber & Eberhard, submitted), 16 male and female characters (Fig. 1) were divided into genitalic traits (1-4), non-genitalic (somatic) traits (5-13) and intermediate traits (14-16) (characters that are close to, or functionally related to the intromittant organs). Measurements were done using a compound microscope with ocular micrometer. Only structures that could be aligned in consistent orientations were measured.

Regression slopes for genitalic on somatic characters ($\bar{Y}_b$=0.35, range 0.17-0.55, N=21) were consistently lower than for somatic on somatic ($\bar{Y}_b$=0.98, range 0.46-1.77, N=36) and genitalic on genitalic characters ($\bar{Y}_b$=0.70; range 0.60-0.87, N=6) (all data log-transformed). Intermediate values were found for regression slopes of genitalia on intermediate traits ($\bar{Y}_b$=0.51, range 0.31-0.69, N=7) and intermediate traits on somatic traits ($\bar{Y}_b$=0.57, range 0.33-0.88, N=15). The same trend has been found in 15 additional species of spiders and insects (Eberhard *et al.*, submitted). This difference in allometry may reflect selection favoring individuals with genitalic traits of average size. This suggests that, if other complicating factors such as pleiotropy are not important, there is at present stabilizing selection on the size components measured of genitalia and relatively high developmental stability (points 3 and 4 in Table 1).

Fluctuating asymmetry (FA; deviations from perfect bilateral symmetry that are thought to reflect the degree of developmental stability) was measured for the first time in genitalic characters and the first time in spiders. FA was not higher in genitalic (1-3) than in somatic (5,7,8,10,11) and one intermediate (15) traits (means of relative FA ranged from 0.8% to 1.1% in genitalic, from 0.4% to 1.3% in somatic
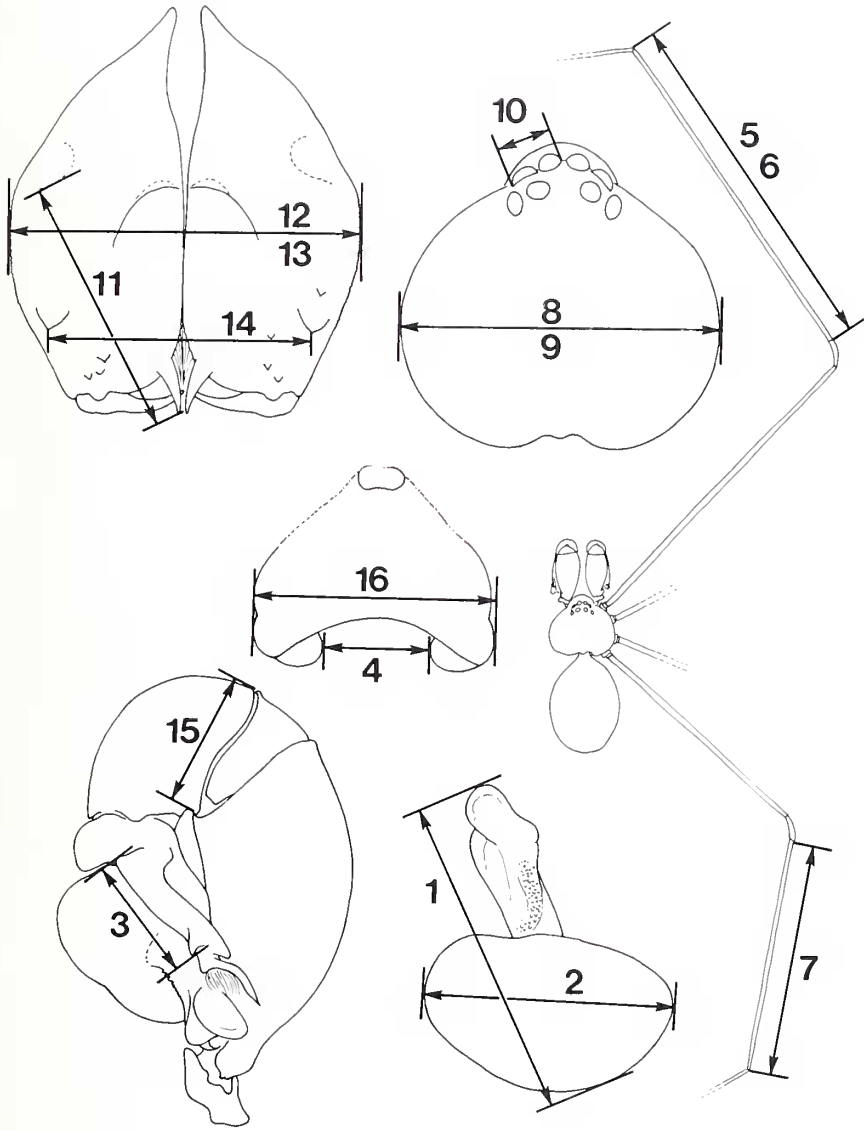
FIG. 1

Measured characters of *Physocyclus globosus*. (1) bulbus length, (2) bulbus width, (3) procursus length, (4) epigynum inner width, (5) and (6) male and female tibia I length, (7) male tibia IV length, (8) male carapace width, which was devided into right and left half, (9) female carapace width, (10) distance between ALE and AME (in male), (11) male cheliceral length, (12) and (13) male and female cheliceral width, (14) distance between male cheliceral apophyses, (15) diameter of male pedipalpal tibia, (16) epigynum outer width.

traits, and was 0.7% in trait 15), which sheds doubt on the general statement that sexually selected traits show higher FA than other morphological characters (point 5 in Table 1). An alternative possibility is that I only measured size components that are currently not under sexual selection and that other aspects of genitalic form might have shown higher degrees of FA. Nevertheless, given the fact that directional selection produces high asymmetry (PALMER & STROBECK 1986) the low degrees of FA strengthen the idea that the measured size components of genitalia may be, at present, under stabilizing selection (see above).

The relationship between degree of FA and size of the trait (point 6 in Table 1) was flat in most genitalic and non-genitalic traits. However, in the highly enlarged male pedipalps there was a significant negative correlation between diameter of tibia and absolute FA (least squares linear regression; b= - 0.07; p=0.0016). This may be interpreted as an indication that pedipalpal strength is a reliable signal of male quality, where only 'high-quality' males are able to develope large and symmetric pedipalps. Pedipalp function during copulation in *Physocyclus globosus* and some other pholcids (UHL *et al.* 1995; HUBER 1995) as well as the fact that the proximal pedipalpal segments are packed with the strongest muscles in the whole spider, suggest female choice for male vigour as an underlying selective force. Thus the proximal pedipalpal segments (that carry the genital bulb, yet are not genitalia sensu stricto) apparently behave as 'secondary sexual traits' regarding points 6 and 7, but as 'other morphological traits' regarding points 1, 2, 4, 5. The inadequacy of Table 1 becomes especially evident when considering the selection to which the trait is subjected (point 3): the low degree of FA

TABLE 1

Differences between 'secondary sexual traits' and 'other morphological traits' following MØLLER (1993), and characterization of the measured genitalic traits in *Physocyclus globosus*.

	'sec. sex. traits'	'other morph. traits'	genitalic traits in *Physocyclus globosus*
1. "intricacy of design"	high	low	low (1,2,4) to medium (3)
2. species-specificity	high	low	high
3. selection to which trait is subjected	directional	stabilizing	stabilizing directional: 2?
4. developmental stability	low	high	high
5. degree of fluctuating asymmetry (FA)	high	low	low
6. relationship between degree of FA and size of trait	linear (pos. or neg.)	u-shaped or flat	flat: 1;3 negative: 2
7. "functional importance"	low	high	low

suggests stabilizing selection, the negative relationship between degree of FA and size of the trait suggests directional selection. A similar negative correlation between trait size and absolute FA was found in bulbal width (b= - 0.18; p=0.0025). This suggests selection on the amount of sperm and/or seminal products that is transferred. But again, the low degree of FA seems not typical of directional selection. Thus, with the existing data set, point 3 may not be solvable for these traits.

GENITALIA AS MULTIFUNCTIONAL ORGANS

This mixed and inconsistent pattern might provide a basis for a substitution of the traditional classification of sexual traits into 'primary' and 'secondary' sexual traits by a classification into 'displaying' (including display in male-male combat as well as external and internal courtship) and 'coupling' traits. 'Coupling traits' include characters whose proper function is confined by some degree of fit with female structures: clamping devices, sperm-transfer and -removal structures, plug-deposition and -removal structures, etc. It is probable that morphologically complex genitalia (like those of many arthropods) will often not be assignable to one of these categories as a whole, but may present 'displaying' as well as 'coupling' (and intermediate) traits , each selected separately, and may thus combine features of 'secondary sexual traits' and 'other morphological traits'.

In addition, inconsistent patterns between species or populations of one species may be expected, depending on their position in the 'epigenetic landscape': populations/species on adaptive slopes, with genetic constitutions far from the equilibrium and with low developmental homeostasis (e.g. small isolated, or peripheral populations) may have genitalia subject to directional selection, with high fluctuating asymmetry, low developmental stability and high variability (as found e.g. in the bug *Eurygaster integriceps* by KERKIS 1931). Populations/species on adaptive peaks on the other hand may show the opposite pattern, as found in the spider in this study.

Thus, a single 'genitalic pattern' may not exist, first because individual structures of a genitalic organ may be subject to different selective regimes, and second, because selection on a particular structure need not be consistent with time.

In conclusion, generalizations of results from studies of displaying traits to all sexually selected traits may be misleading (Tadler, pers. comm.). Zoologists focussing on sexual selection ought to bear in mind EBERHARD's (1993) claim that "...genitalic evolution...should be taken into account in any discussion of sexual selection that aims at generality".

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